

RHEOTROPISM IN *UROSALPINX CINEREA* SAY.¹

H. FEDERIGHI.

UNITED STATES BUREAU OF FISHERIES.

Rheotropism has been observed in many animals (Schulze, 1870; Parker, 1903, 1908; Lyon, 1904; Jennings, 1904; Dimon, 1905; Hadley, 1906; Allee, 1912; Jordan, 1917; Arey and Crozier, 1919, 1921), and the receptors for this response appear to vary in the different species. Stahl (1884, from Verworn, 1899) and Verworn (1899) believed rheotaxis to be a positive response to pressure stimulation, a theory that was used by Wheeler (1899) to explain anemotropism as a special form of rheotropism. According to Schulze (1870) and Bonnier (1896) the reaction in fishes is brought about by the stimulation of the lateral line organs, an interpretation that was shown to be untenable for *Fundulus heteroclitus* (Parker, 1904) and for *Epinephelus striatus* Bloch (Jordan, 1917), where the organs of touch serve also as the essential organs of stimulation by water currents. Tullberg (1903) eliminated the ear of fishes and found that the animals operated upon were insensitive to water currents, from which he assumed that the ear was the receptor for this response. To this theory there are serious objections, as was pointed out by Parker (1903). A theory first proposed by Lyon (1904, 1909) and accepted by Loeb (1918) stated that in fishes "the primary cause of orientation in streams of some uniformity of motion is an optical reflex, a tendency on the part of the animals to follow the field of vision. . . . The essential element of stimulation is the environment not the current. . . . Contact between the fishes and stationary objects may lead to orientation. . . . In violent streams. . . . the fish may be oriented without sight or contact with solid objects. . . . here. . . . relative velocities constitute the essential elements of stimulation. If part of the water moves, and the next to it is

¹ Published by permission of the United States Commissioner of Fisheries

relatively at rest, the fish may respond just as it does to contact with solids" (Lyon, 1904). "Fish with one eye blinded react to currents of water like normal fish. The usual form of stimulation is visual. The fish turn the nearest way to face the current, whether in so turning the motion be toward or from the injured side. . . . It seems to the writer impossible to bring these observations into accord with the tropism scheme of one-sided response to one-sided stimulation" (Lyon, 1909). Hadley (1906, 1908) showed that the lobster is rheotactic during its free swimming larval stage and by moving the environment rather than studying the animals in a current he showed that the optical stimulus alone is capable of producing this reaction. He adds that the rheotactic reaction *induced by currents* is more definite at night, tending to show that this is not optical. Main (1928) in the course of some experiments on the phototropism of fishes states "fish do not orient themselves in such fashion as to keep the *static* visual field the same."

In the literature on rheotropism there are no quantitative data available such as obtain for phototropism and geotropism. This may be due to the fact that the animals so far investigated have not permitted this type of study. For instance, it would be difficult to determine the rate of orientation of a fish in a stream of a given velocity. In a snail such as *Urosalpinx cinerea*, on the other hand, we have an animal that not only exhibits a precise and immediate reaction to water currents but is also admirably suited to quantitative study.

The following is a report of some observations on the effect of a current upon the movements of *Urosalpinx cinerea*. The interest of the data lies in the fact that this animal in its behavior to currents appears to follow Loeb's (1918) theory of tropistic conduct. Hitherto it has been impossible to interpret the reaction of animals to currents as a simple tropistic response (Lyon, 1909).

If *Urosalpinx cinerea* is placed in a current of water it orients itself so that the siphon is pointing upstream and then moves against the current. The response is definite and immediate. The removal of the eyes or of the tentacles does not disturb the precision and character of this reaction. Furthermore, light does not interfere with the orientation and movement, since experiments

carried on in the darkroom give results similar to those obtained in daylight. From these preliminary and general observations the work was expanded to include the following: (1) a study of the relation between the rate of current and the rate of creeping; and (2) a study of the relation between the rate of current and the rate of orientation (turning).

The apparatus used in these experiments consisted of a celluloid trough 2" x 2" x 20", open at either end and suspended in a water current on an even keel so as to eliminate geotropic effects. Figure 1 gives two views of the apparatus and shows the direction of flow of the current. The lower view (1) shows a longitudinal half of the apparatus. The upper sketch (2) is a top view of the apparatus. The arrows indicate the direction of the flow of water in the various parts of the two troughs.

The rate of the water current was determined by noting the time necessary for uniformly-sized bits of cork to travel five inches. Fifteen to twenty readings were taken for each velocity. These were averaged and the figure thus obtained was used as the surface velocity of the current, from which the bottom velocity was determined (Gibson, 1925). Surface velocities from 1.25 to 7.60 cm. per second were used. The water temperature was kept constant by means of a thermostat, to within $\pm 2^\circ$ Centigrade. The current was of the turbulent type, the only kind obtainable under these conditions.

The experimental animals were chosen for the definitiveness of their response alone, no attempt being made to obtain animals of the same size. Such selection is not only permissible but desirable (*cf.* Crozier, 1928). In all, twenty-five animals were used; eleven for the observations on the rate of turning, and fourteen for the experiments on the rate of creeping.

The data for the two series of experiments were collected in different ways. For the study of the relation between the rate of current flow and the rate of creeping, the time necessary for the animal to creep one half inch, directly against the current, was taken as a measure of the response. The procedure was as follows: after the desired current velocity had been obtained the animal was placed in the trough *B*. In a short while the animal would orient and begin creeping against the current. The time

(with a stop watch) necessary for it to creep one half inch was then noted. Since only those readings in which the animal crept actively and without apparent interruption were used, a mark on the shell was made to determine when the required distance had been traversed. Observations in which the animal pushed its shell forward without any actual translatory movement of the pedal mass were discarded. There were other factors which at times influenced the rate of creeping. For instance, the animal would sometimes veer off and strike the sides of the trough, and

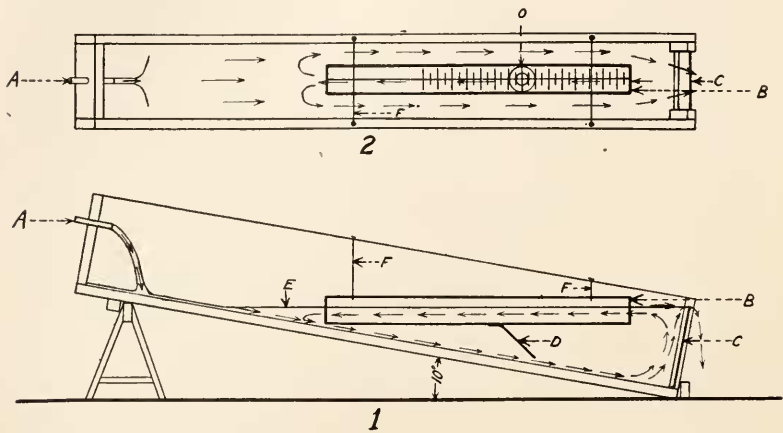


FIG. 1. Top (1) and side (2) views of apparatus. *A*, water inflow from coils placed in constant-temperature bath; *B*, celluloid experimental trough; *C*, glass front of outer tank; *D*, mirror at 45° angle to bottom of *B*; *E*, water level; *F*, wires supporting *B* on even keel; and *O*, system of circular and radial coördinates by which path taken by animal was copied.

occasionally a small mass of foreign substance resting on the bottom would interfere. All these records were disregarded. In a short while one could easily distinguish when the animal was moving actively and uninterruptedly. After each reading it was lifted from the substratum and the slime track cleaned away. In this way the influence of a previous track upon the movements of an animal was obviated. After approximately two to three minutes the next record was made. On the average ten readings were taken for each animal.

For these experiments fourteen animals were used, for which thirty-five satisfactory series of observations were made. In all

three hundred creeping rates at twenty-five different current rates were collected for the fourteen animals. Fig. 2 shows the results graphically when the current rate is plotted against the rate of creeping, both in inches per second.

Some slight but necessary modifications in procedure were made in the experiments on the effect of the current rate upon the rate of turning, but before giving these a word of explanation as to the apparatus is necessary. In Figure 1 (top view) there is seen the inner celluloid trough, in about the center of which are two concentric circles with perpendicular diameters. Immediately under this [as can be seen in the longitudinal section (2)] is placed a mirror (*D*) at an angle of 45° to the bottom of the trough. If one looks through the glass side (*C*) of the outer trough at the mirror (*D*) he sees reflected on the mirror the concentric circles (*O*). Thus when an animal is placed on "*O*," by

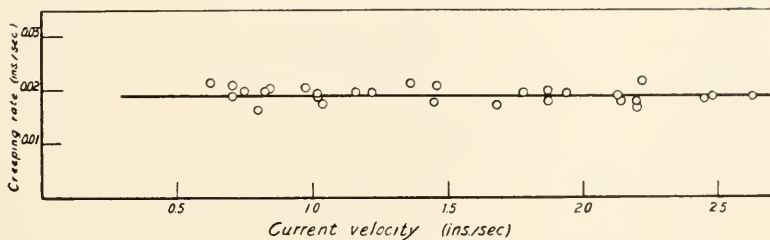


FIG. 2. Graph showing the relation between the rate of creeping and the surface current velocity both in inches per second.

looking through "*C*" at "*D*" one can observe the movements of its pedal surface. By the use of a similarly prepared record sheet the path of the animal is easily traced and a true record of the path of the animal's movements obtained.

The animal was placed at "*O*" and as soon as it began to creep and orient, its path was copied on the record sheet by observing continuously the path taken by a point on the pedal surface immediately behind the anterior transverse ridge, and a record was made of the time necessary for this movement. After each observation the slime track was removed. At least ten records were made for each animal. These were then measured for the total length of path and for the angular displacement of a tangent to the path, giving therefore three sets of figures for each trail: (1) the

total length of path; (2) the time required for such movements; and (3) the total number of degrees turned.

For these observations eleven animals were used at six different rates of current for a total of three hundred and two records. The results are shown in Fig. 3, where the square of the bottom

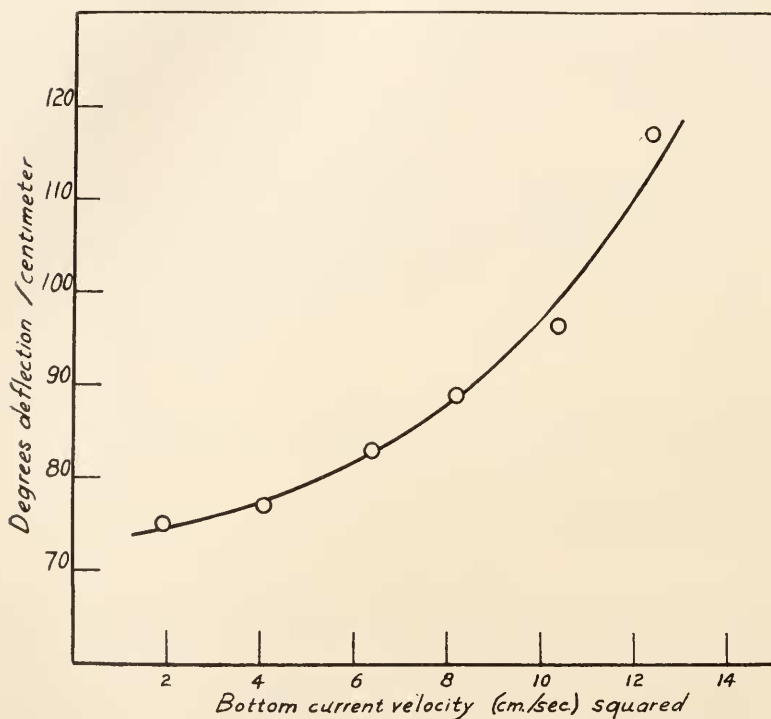


FIG. 3. Graph showing the relation between the bottom current velocity (cm./sec.) squared (Intensity) and the degrees deflection per centimeter of path (Effect).

current velocity is used as a measure of the intensity of stimulation and the degrees deflection per centimeter of path is a measure of the effect produced.

It is seen that the degrees turned per centimeter of path is a function of the rate of water current and that the curve (Fig. 3) is possibly the lower half of the S-shaped curve that one often obtains when the effect is plotted against the intensity (Hecht, 1922-23; Crozier, 1928). It was impossible to obtain points for

current rates higher than 7.60 cm. per second (at the surface) because above this the animal does not exhibit precise orientation and furthermore the stronger currents sometimes lift the animal from the substratum and passively wash it away. The receptors for this response seem to be the proprioceptors located in the symmetrical parietal muscles. The unequal tension on these muscles, produced by the pull of the shell which in a stream tends to straighten out so that the shell presents the least resistance to the

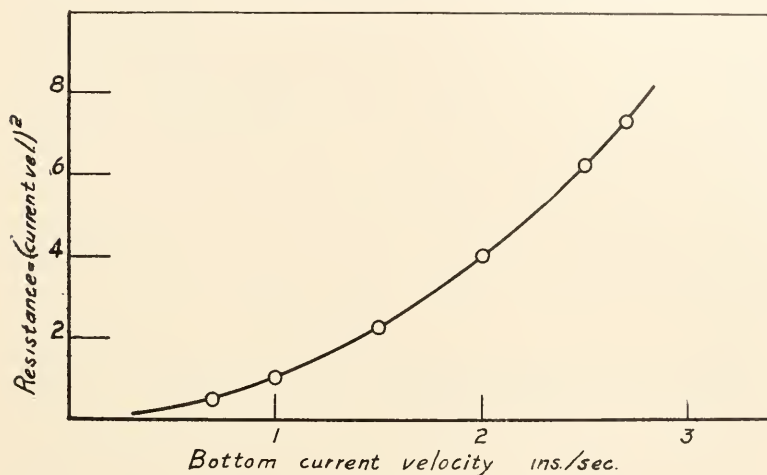


FIG. 4. Graph showing the relation between the bottom velocity in inches per second and the resistance overcome by the animal creeping against the current.

flow of water turning with the foot-mass as a pivot, is the stimulus which brings about orientation. This seems to be the same mechanism that functions in the geotropism of certain animals where it is proposed that the gravity responses depend on the stimulation of the proprioceptors in the parietal elements (Cole, 1925-26; Crozier and Federighi, 1924-1925; Wolf, 1926-1927; Crozier, 1928).

Whether the mechanism of creeping in *Urosalpinx cinerea* is the ciliated epithelium of the pedal surface (Copeland, 1919, 1922), or whether creeping is due to "arhythmic" pedal waves (Parker, 1911; Crozier, 1919) it is evident that the rate of creeping is not affected by the velocity of the current (Fig. 2). It

is necessary however to note that although the rate of creeping is constant the resistance overcome is greater as the current-rate increases. Thus the animal must do more work as the velocity increases in order to maintain its uniform rate of progression since the pressure exerted by a flowing stream of water is proportional to approximately the square of the velocity (Gibson, 1925). In other words, since in the results all other factors remain constant and only the resistance overcome or the pressure exerted by the flowing stream varies as the current varies, this may be taken as a measure of the effect produced upon the animal. In Fig. 4 these derived data are given in graphical form. The effect is given as the pressure exerted by the flowing stream of water (resistance overcome) which is equivalent to the square of the current velocity; the intensity of stimulation is given as the bottom current velocity. This means that if the resistance overcome by the animal is taken as a measure of the effect produced, then the effect is proportional to the square root of the current velocity.

These conclusions are important because for the first time it has been shown that the orientation and the creeping of an animal in a water current is a function of the intensity of the current. It has been possible to measure both intensity and effect and to show that: (1) the rate of turning is a function of the current velocity, and if these are plotted there is obtained a curve which is similar to that obtained for other intensity *vs.* effect curves; and (2), the rate of creeping is independent of the current rate, but if one takes the resistance overcome rather than the rate of creeping as a measure of the effect then the effect is proportional to the square root of the current velocity.

SUMMARY.

If *Urosalpinx cinerea* Say is placed in a current of water it will orient and move against the current. It has been possible to measure the rate of turning and the rate of creeping at various current rates. These results indicate that the rate of turning (degrees deflection per centimeter of path) is a function of the current velocity and that when plotted respectively as effect and intensity the curve obtained follows the usual effect *vs.* intensity curve obtained for other tropistic reactions. The organs of

stimulation for this response seem to be the proprioceptors in the symmetrical parietal musculature of the animal. Although the rate of creeping is independent of the rate of current, the amount of resistance overcome (or the work done) is also a function of the current velocity.

CITATIONS.

Allee, W. C.

- '12 An Experimental Analysis of the Relation between Physiological States and Rheotaxis in *Iso-poda*. Journ. Exp. Zool., Vol. 13, pp. 269-344.

Arey, L. B., and W. J. Crozier.

- '19 The Sensory Responses of *Chiton*. Journ. Exp. Zool., Vol. 29, pp. 157-260.

Arey, L. B., and W. J. Crozier.

- '21 On the Natural History of *Onchidium*. Journ. Exp. Zool., Vol. 32, pp. 443-502.

Bonnier, P.

- '96 Sur les sens latéral. Compt. rend. soc. biol., sér. 10, T. 3, pp. 917-919.

Cole, W. H.

- '25-'26 Geotropism and Muscle Tension in *Helix*. Journ. Gen. Physiol., Vol. 8, pp. 253-263.

Copeland, M.

- '19 Locomotion in Two Species of the Gastropod Genus *Alcctrion* with Observations on the Behavior of Pedal Cilia. Biol. Bull., Vol. 37, pp. 120-138.

Copeland, M.

- '22 Ciliated and Muscular Locomotion in the Gastropod Genus *Polinices*. Biol. Bull., Vol. 41, pp. 132-142.

Crozier, W. J.

- '19 On the Use of the Foot in Some Mollusks. Journ. Exp. Zool., Vol. 27, pp. 359-366.

Crozier, W. J.

- '28 Tropisms. Journ. Gen. Psychol., Vol. I., pp. 213-238.

Crozier, W. J., and H. Federighi.

- '24-'25 Phototropic Circus Movements of *Limax* as Affected by Temperature. Journ. Gen. Physiol., Vol. 7, pp. 151-169.

Dimon, A. C.

- '05 The Mud Snail: *Nassa obsoleta*. Cold Spring Harbor Monographs, No. 5, 48 pp.

Gibson, A. H.

- '25 Hydraulics and its Applications. 3d Ed., xv + 801 pp. New York.

Hadley, P. B.

- '06 The relation of optical Stimuli to Rheotaxis in the American Lobster, *Homarus americanus*. Amer. Journ. Physiol., Vol. 17, pp. 326-342.

Hadley, P. B.

- '08 The Behavior of the Larval and Adolescent Stages of the American Lobster (*Homarus americanus*). Journ. Comp. Neur. and Psychol., Vol. 18, pp. 199-301.

Hecht, S.

- '22-'23 Sensory Adaptation and the Stationary State. Journ. Gen. Physiol., Vol. V., p. 555.

Jennings, H. S.

- '04 The Behavior of *Paramecium*. Additional Features and General Relations. Journ. Comp. Neur. and Psychol., Vol. 14, pp. 441-510.

Jordan, H.

- '17 Rheotropic Responses of *Epinephelus striatus* Bloch. Amer. Journ. Physiol., Vol. 43, pp. 438-454.

Loeb, J.

- '18 Forced Movements, Tropisms, and Animal Conduct. Monographs on experimental biology. 209 pp. Philadelphia.

Lyon, E. P.

- '04 On Rheotropism. I. Rheotropism in Fishes. Amer. Journ. Physiol., Vol. 12, pp. 149-161.

Lyon, E. P.

- '09 On Rheotropism. II. Rheotropism of Fish Blind in One Eye. Amer. Journ. Physiol., Vol. 24, pp. 244-251.

Main, R. J.

- '28 Phototropism in Fishes, and its Relation to the Results Obtained by Eye-dislocation. Zeitschr. f. vergl. Physiol., Bd. 7, s. 611-616.

Parker, G. H.

- '03 The Sense of Hearing in Fishes. Amer. Nat., Vol. 37, pp. 185-204.

Parker, G. H.

- '04 Hearing and Allied Senses in Fishes. Bull. U. S. Fish Comm. (1902), Vol. 12, pp. 45-64.

Parker, G. H.

- '08 The Sensory Reactions of *Amphioxus*. Proc. Amer. Acad. Arts and Sci., Vol. 43, pp. 415-455.

Parker, G. H.

- '11 The Mechanism of Locomotion in Gastropods. Journ. Morph., Vol. 22, pp. 155-170.

Schulze, F. E.

- '70 Ueber die Sinnessorgane der Seitenlinie bei Fischen und Amphibien. Arch. f. mikr. Anat., Bd. 6, s. 62-88.

Tullberg, T.

- '03 Das Labyrinth der Fische. Bihang K. Svenska Vet. Akad. Handlingar, Stockholm, Bd. 28, No. 15.

Verworn, M.

- General Physiology. Trans. by T. S. Lee. From 2d German Edition. xvi + 615 pp. New York.

Wheeler, W. M.

- '99 Anemotropism and Other Tropisms in Insects. Arch. f. Entwickl.-mech., Bd. 8, s. 373-381.

Wolf, E.

- '26-'27 Geotropism in *Agriolimax*. Journ. Gen. Physiol., Vol. X., pp. 757-765.